# The spiral cords and the internal denticles of the outer lip in the Muricidae : terminology and methodological comments

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**KEYWORDS.** Muricidae, spiral sculpture, terminology, description, homology.
**MOTS-CLEFS.** Muricidae, sculpture spirale, terminologie, description, homologie.

**ABSTRACT.** The muricid spiral sculpture is organized in two major character complexes : the spiral cords and the internal denticles of the outer lip. The identity of the characters is researched by their topological and ontogenetical correspondences, then codified in a terminology. This new descriptive method allows to clarify the presentation of the characters and to propose structural homologies. It has been used by Merle (1999) to study the adaptative radiation of the Paleogene muricids, particularly to analyze the evolutionary processes implicated in the sculptural modifications of the Muricopsinae. The english translation of this terminology is here given, with some methodological comments.

**RESUME.** La sculpture spirale des Muricidae est organisée en deux complexes majeurs de caractères : les cordons spiraux et les dents internes du labre. L'identité des caractères est recherchée par leur correspondances topologique et ontogénétique, puis codifiée dans une terminologie. Cette nouvelle méthode descriptive permet de clarifier la présentation des caractères et de proposer des homologies primaires. Elle a été utilisée par Merle (1999) pour étudier la radiation adaptative des Muricidae paléogènes, en particulier pour analyser les processus évolutifs impliqués dans les changements de sculpture des Muricopsinae. Le présent article donne la traduction anglaise de cette terminologie avec quelques commentaires méthodologiques

## INTRODUCTION

The muricids show a great morphological diversity, mainly expressed by the variable number, the morphology and the arrangement of the spiral elements (cords, spines, denticles...). It results to an evolution of about 70 millions years, but the evolutionary mechanisms and processes leading to this sculptural diversity remain poorly studied, despite a rich corpus of description.

The spiral sculpture is often used to give taxonomic distinctions at different hierarchic levels (specific, generic or subfamilial levels). However, Hylleberg & Nateewathana (1992) pointed that the spiral characters are not clearly identified, resulting to a potential difficulty to recognize or to compare muricid taxa when they are used. According to Hylleberg & Nateewathana (1992), I noted (Merle, 1999) that the traditional descriptive method does not propose a real comparative morphology approach, including the identity of the spiral characters. In other words, I conclude that the concept of homology has been unsufficiently applied for this kind of characters. These methodological comments also fully explain why the evolutionary changes of the muricid spiral sculpture still remains so obscure, because these changes cannot be accurately studied without morphological analyses researching structural homologies.

In other gastropods families, several examples showing the research of the identity of the spiral characters have been given by Bieler (1988, 1995) for the Architectonicidae and the Mathildidae, Marshall (1995) for the Calliostomidae and Allmon (1994) for the Turritellidae (the list of the examples is not exhaustive). The characters are identified by different criteria (topological and ontogenetical correspondences) and codified in a terminology. For the authors, this approach allows to postulate hypotheses of structural homology, useful for subsequent analyses [morphological comparisons for traditional systematics (Bieler 1995 ; Marshall, 1995), primary homologies for cladistic analyses (Bieler, 1988 ; Allmon, 1994) and heterochronic evolution of the spiral characters (Allmon, 1994). A same approach has been used by Merle (1999) to study the adaptative radiation of the Paleogene muricids, and particularly to detect the evolutionary processes implicated in the sculptural changes of the Muricopsinae. The purpose of the present paper is to give the english translation of this terminology with some methodological comments (principes and protocoles) on the identification of the spiral characters. An extended discussion of the methodology will be the object of a future paper (Merle in prep.). This paper also contains numerous figures showing these identifications, because they correspond to the necessity of a clear presentation of the characters. By this way, a real checking and a discussion on the identified characters may be scientifically discussed.

### Abbreviations

DME : D. Merle coll. ; JT : Jean Trondle coll. ; LDO : Luc Dolin coll. ; MNHN-BIMM, Muséum National d'Histoire Naturelle, Paris (Laboratoire de Biologie marine et Malacologie ; MNHN-LP, Muséum National d'Histoire Naturelle, Paris (Laboratoire de Paléontologie) ; NHM : Natural History Museum, London ; RH : Roland Houart ; USNM : U.S. National Museum, Washington.

## PRINCIPES AND PROTOCOLES

**Principes** : in comparative morphology, the identification of the characters is basically the first stage to propose structural homologies (or primary homologies *sensu* de Pinna, 1991). To propose structural homologies, Patterson (1982) recommends to respect three congruence criteria in the characters analyses : 1°) similarity of the characters ; 2°) non co-existence of the characters, 3°) similar topographical or topological correspondence. Merle (1999) added the ontogenetical correspondence following Marshall (1995).

1°) Similarity of the characters : regarding this criterium, the characters related to the spiral sculpture may be divided in three major complexes : 1°) the spiral cords on the dorsal face and their connected axial expressions (spines and nodes) ; 2°) the internal denticles of the outer lip ; 3°) the ornements (tubercules or folds) of the inner lip. In this paper, the two first complexes (spiral cords and internal denticles of the outer lip) are presented.

2°) Non co-existence of the characters and serial homology : the non co-existence criterium is problematic, because in a given complex (eg. : spiral cords), the characters co-exist, are built with the same constructional plan, have more or less a similar morphology, and each one corresponds to an element of the serie. This kind of characters is called a serial homology. Despite their co-existence, the spiral cords are placed on different topological alignments and they are not generated by other cords. To give an example, the muricid shoulder cord appears independently of that of the siphonal canal cords. Because of their independance (Merle & Pacaud, in press, Merle, Guarrigues and Pointier, 2001) and their limited number, the major characters of the spiral sculpture (primary and secondary cords and denticles of the outer lip) may be identified in many cases. It is also important to note that this opportunity has been previously explored in holostomatous gastropods (Turritellidae, Mathildidae, Architectonicidae), in which the number of cords is less numerous than in the Muricidae.

3°) Ontogenetical correspondence : in the traditional descriptions, the adult morphology is only described. For the spiral cords, the descriptions consist to categorize the cords with a preeminence criterium (Radwin & D'Attilio, 1976). By this way, the primary cords are more preeminent than the secondary cords, which are themself more preeminent than the tertiary cords. This criterium excluding the ontogenesis is inacurate to correctly identify the cords for two reasons. Firstly, the appearance of the spiral cords is organized in several sequences (or orders). Consequently, to identify the cords without observing their appearance sequence may potentially generate mistakes, because the cords belonging to different appearance sequences are not homologous. Secondly, the adult morphology of the cords represents a strong pittfall to identify the cords, because the relief may change during the ontogenesis. For example, a cord belonging to the first appearance sequence can have the same relief of another cord belonging to the second appearance sequence, because its growth is decelerated during the ontogenesis, and conversely. Several observations of these ontogenetical changes has been illustrated for the Muricopsinae (Merle, 1999, fig. 31 with the example of *Xastilia kosugei* Bouchet & Houart, 1994) and for the muricine genus *Siratus* Jousseaume, 1880 (Merle, Guarrigues and Pointier, 2001).

4°) Topological correspondence : when the appearance sequence of the spiral cords is identified, the topological places can be researched. The methodology is not different than that given for other families (ex. : Architectonicidae, Mathildidae), and consist to detect all topological places. When all places are detected, the topological correspondence and the primary homologies may be proposed. In the case of the muricids, the spiral sculpture is characterized by one very stable topological point, the shoulder cord (= P1). It belongs to the primary cords group, and by a keel, divides the dorsal face of the shell in two parts : the infrasutural ramp and the convex part of whorl. Because of its low variation, the shoulder cord may also be regarded as a reference point.

**Protocole** : considering these observations, a protocole containing three points is proposed to identify the characters. 1°) The cords are characterized by their appearance sequence, because we reject the inacurate preeminence criterium.

Consequently, the primary cords correspond to the first appearance sequence, the secondary cords to the second...2°) All topological places are researched in the smallest juvenile morphologies (see an example Figs 13-14, with *Murexsul elatospira*) to detect the whole primary sequence of cords. 3°) The most sculptured morphologies of the family are used, but less ornemented muricids, such as *Poirieria* Jousseaume, 1880 (Fig. 9B), *Flexopteron* Shuto, 1969 (Fig. 9C), *Paziella* Jousseaume, 1880 (Fig. 10B, E), the Typhinae (Figs. 11, 12A-C), the Trophoninae (Fig. 12D-E) and the Ocenebrinae (Fig. 18) also have been examined. The most sculptured muricids mainly occur in the modern Muricinae [eg : *Murex* Linnaeus, 1758 (Fig. 9D), *Chicoreus* Montfort, 1810 (Fig. 9A), *Homalocantha* Mörch, 1852 (Fig. 10B-C, E), *Hexaplex* Perry, 1811 (Fig. 10F) and *Siratus* (see figures in Houart, 2000 and in Merle, Guarrigues and Pointier, 2001], the Muricopsinae (Figs. 13-17) [*Muricopsis* Bucquoy & Dautzenberg, 1882 (Fig. 15A-C) and *Favartia* Jousseaume, 1880 (Fig. 17A-B, F)], and also in the Ergalataxinae (Fig. 19) and the Rapaninae (Fig. 20).

**PRIMARY CORDS**

Using the given protocole, fourteen topological places have been registred at the level of the primary cords (Table 1 and Fig. 1). They correspond to the maximum number of the observed topological places including the numerous siphonal canal cords seen in *Murex*, but provisionally excluding these of *Murex pecten* Lightfoot, 1786 and other similar species, because we lack sufficiently young *M. pecten* to verify if all major cords really are ontogenetical primary cords. Three places groups may be distinguished : 1°) the sutural ramp, 2°) the convex part of the whorl and 3°) the siphonal canal (Fig. 1).

1°) Sutural ramp cord group : this group contains the most adapical primary cords and two topological places (1 and 2 = SP and IP) have been registred. They are invariably placed on the sutural ramp (Fig. 2). The topological place 1 (= SP) corresponds to the sutural cord, also described by Vermeij (1995).

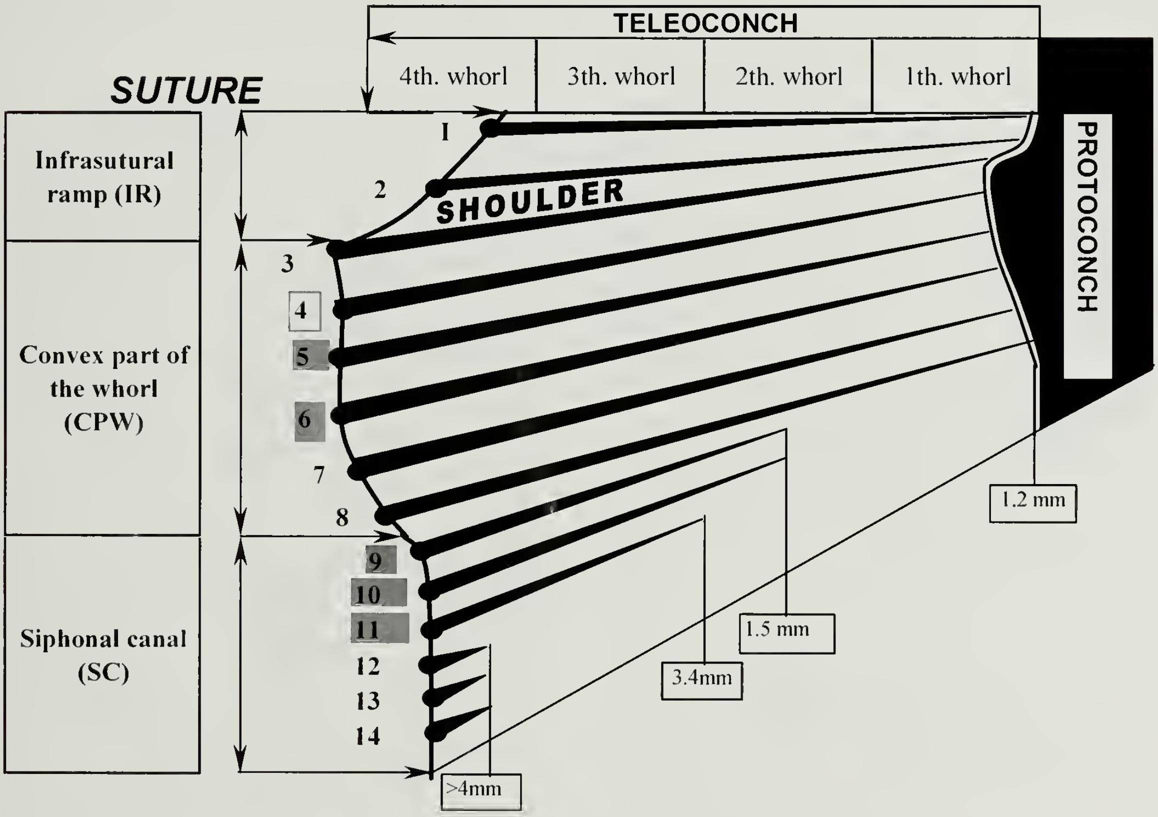
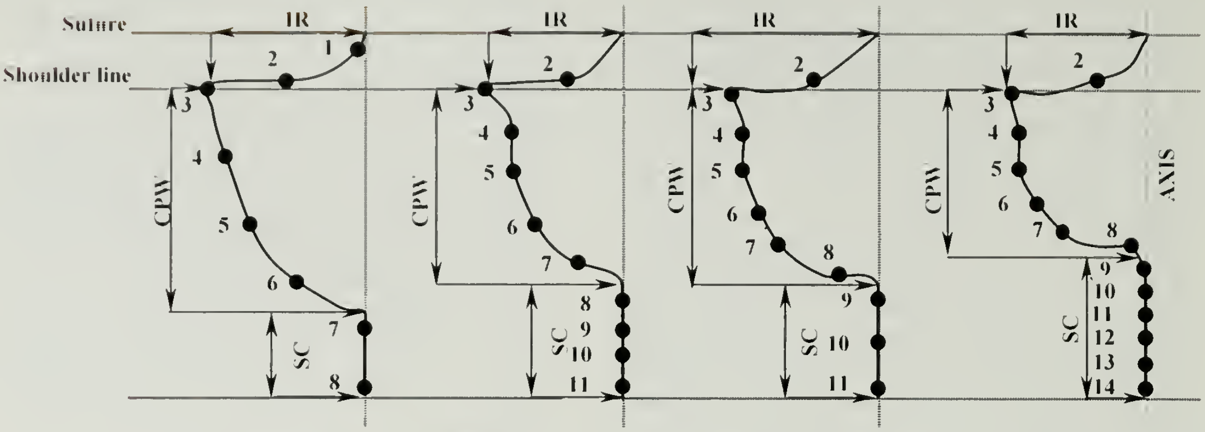


**Figure 1** : Composite muricid showing the maximum precocity of the primary cords (dorsal view). Main informative species : topological point 1 (= SP) : *Stramonita haemastoma* (Linnaeus, 1767), Recent ; topological point 2 (= IP) : *Muricopsis (Risomurex) withrowi* Vokes and Houart, 1986, Recent ; topological points 3 to 8 (= P1 to P6) : *Murexsul elatospira* (Cossmann & Peyrot, 1924), Chattian ; topological points 9 to 10 (= ADP to MP), see also Figs 13-14 : *Murexsul rostralis* (Grateloup, 1847), Chattian ; topological point 11 (= ABP) : ?*Murexsul* sp. Vokes, 1994, Ypresian ; topological points 12 to 14 (EAB to EAB3) : *Murex tribulus* Linnaeus, 1758, Recent, see also Fig. 9D.



*Drupa* and *Orania*

*Muricopsis* and *Favartia*

*Chicoreus*, *Ocenebra* and *Trophon*

*Murex*

**Figure 2** : Schematic drawings showing the places and the topological correspondences of the primary cords in the most sculptured muricids (dorsal view). *Drupa* Röding, 1798 (Rapaninae), see also Fig. 20D ; *Orania* Pallary, 1900 (Ergalataxinae), see also Fig. 19A-C ; *Muricopsis* Bucquoy & Dautzenberg, 1882 (Muricopsinae), see also Fig.15 A-C ; *Favartia* Jousseaume, 1880 (Muricopsinae), see also Fig. 17A-B, F) ; *Chicoreus* Montfort, 1810 (Muricinae), see also Fig. 9A ; *Ocenebra* Gray, 1847 (Ocenebrinae), see also Fig. 18A, E ; *Trophon* Montfort, 1810 (Trophoninae), see also Fig. 12D-E ; *Murex* Linnaeus, 1758 (Muricinae), see also Fig. 9D. IR = infrasutural ramp ; CPW = convex part of the whorl ; SC = siphonal canal.

2°) Convex part of the whorl cord group : in this second group, the shoulder cord (= P1) is arbitrarely included. Including the shoulder cord, a maximum of six topological places (3 to 8 = P1, P2, P3, P4, P5 and P6) have been found (Fig. 2), but several cords are not always placed on the convex part of the whorl, despite a same topological place. The three adapical places (3 to 5 = P1, P2, P3) are invariably placed on the convex part of the whorl, while the three abapical places (6 to 8 = P4, P5 and P6) can occasionally be placed on the siphonal canal (Fig. 3).

3°) Siphonal canal cord group : this group includes the most abapical primary cords which are invariably placed on the siphonal canal (Fig. 2). A maximum of six topological places (9 to 14 = ADP, MP, ABP, EAB1, EAB2 and EAB3) has been registred. The three most adapical siphonal cords (9-11 = ADP, MP and ABP) are widespread in different subfamilies, such as the Muricinae, the Muricopsinae, the Ocenebrinae and the Trophoninae, while they are rarer (eg. : Rapaninae) or absent (eg. : Typhinae) in the other subfamilies. It is important to stress that the two most abapical places (12 to 14 = EAB2 and EAB3) mainly occur in the genus *Murex*, and are probably autapomorphic (Merle, 1999). We also precise that if *Murex pecten* and related species posses more adapical primary cords than in other species of the genus *Murex*, it will be useful for the terminology to add new topological places, such as EAB4, EAB5 for example.

## SECONDARY AND TERTIARY CORDS

The secondary cords can appear only after the appearance of the primary cords. This appearance modality depends to an absolute priority rule (Grandjean, 1943 ; Bouligand, 1989), and the formation process shows that the secondary cords don't derive from the primary cords (Merle, 1999, figs. 38, 39, 41). In fact, the secondary cords are exactly inserted between two primary cords, and the topological correspondence of each secondary cords may easely be deduced (Table 2 and Fig. 4), when those of the primary cords are delineated.

The formation process of the thrue tertiary cords is similar to this of the secondary cords and when they appear, they are exactly inserted between a primary and a secondary cord. A terminology of the tertiary cords may be used if it is necessary. For example, the two tertiary cords belonging to the space between P1 and P2 and separated by s1 (= P1, *t1d*, s1, *t1b*, P2) may be codified as *t1d* with a *d* for the most adapical cord and *t1b* with a *b* for the most abapical cord. On the other hand, the tertiary cords begin to represent microsculptural spiral elements and they also can co-exist with other fine spiral sculptures, which appear before the formation of the primary and the secondary cords (Merle, 1999, fig. 43). These other microsculptures, frequently finer, cannot be regarded as homologous of the thrue tertiary cords, regarding their appearance modality. A work concerning the spiral microsculptures will be necessary to clarify the homologies found in these fine sculptures, often qualified with the too general term of threads.

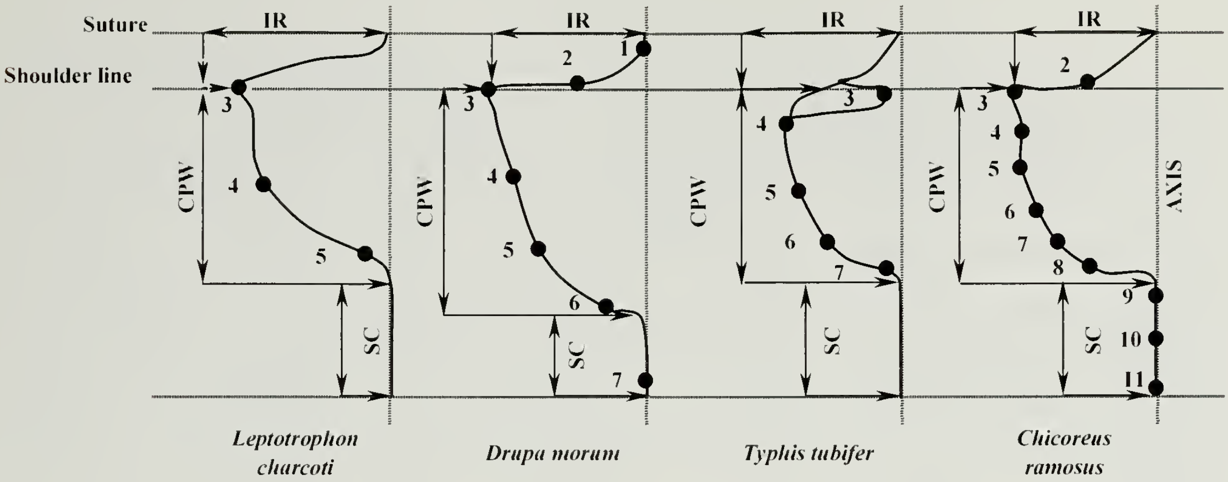


**Figure 3** : Places and topological correspondences of the primary cords for muricid species (dorsal view). They show different places (convex part of the whorl or siphonal canal) for the topological points 6 to 8. *Leptotrophon charcoti* (Houart, 1995), Trophoninae, Recent ; *Drupa morum* (Röding, 1798), Rapaninae, Recent ; *Typhis tubifer* (Bruguière, 1792), Typhinae, Lutetian, see also Fig. 11; *Chicoreus ramosus* (Linnaeus, 1758), Muricinae, Recent. IR = infrasutural ramp ; CPW = convex part of the whorl ; SC = siphonal canal.

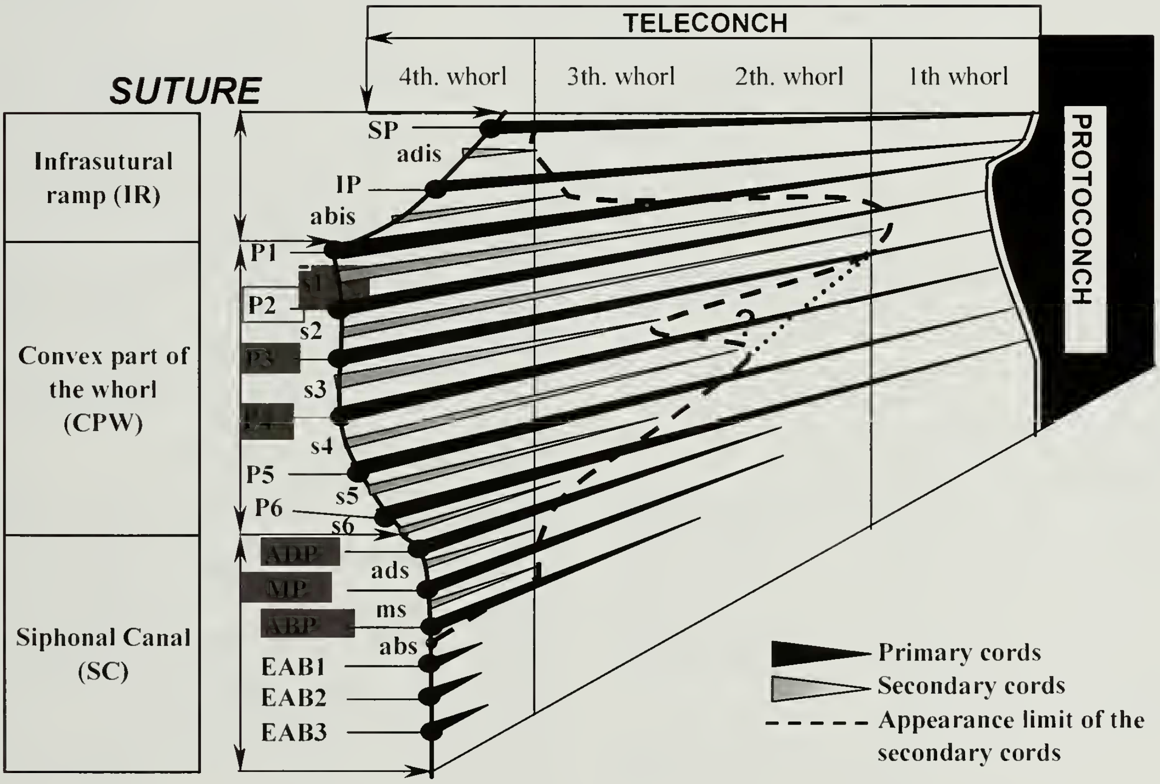


**Figure 4** : Composite muricid showing the maximum precocity of the secondary cords (dorsal view). Main informative species : adis : *Murexsul elatospira* (Cossmann & Peyrot, 1924), 4.5 mm height, Chattian ; abis : *Murexsul prionotus* (Tate, 1888), 4.3 mm height, Priabonian ; s1 : *Haustellum haustellum* (Linnaeus, 1758), Recent ; s2 : *Panamurex aspinosus* (Meyer, 1886), Rupelian ; s3 : *Murexsul rostralis* (Grateloup, 1847), 2.9 mm height, Chattian ; s4 : *M. elatospira*, 2.5 mm height ; s5 : *M. elatospira*, 3.2 mm height ; s6 : *M. elatospira* : 4,9 mm height ; ads and ms : ?*Murexsul* sp. Vokes, 1994, 3.4 mm height, Ypresian ; abs : *Favartia frondosa* (Lamarck, 1803), 14.2 mm height, Lutetian.

| **FRENCH (Merle, 1999)** | | | | **ENGLISH** | | | |
|---|---|---|---|---|---|---|---|
| **CORDONS PRIMAIRES (Figs. 1-3)** | | | | **PRIMARY CORDS (Figs. 1-3)** | | | |
| **Cordons** | **Abreviation** | **Position topologique** | **Emplacement sur la coquille** | **Cords** | **Abbreviation** | **Topological place** | **Place on the shell** |
| Cordon subsutural | **CST** | **1** : adapical à CIF | Rampe infrasuturale (sous la suture) | Subsutural cord | **SP** | **1** : adapical to IP | Infrasutural ramp (below the suture) |
| Cordon infrasutural | **CIF** | **2** : entre CST et C1 | Rampe infrasuturale | Infrasutural cord | **IP** | **2** : between SP and P1 | Infrastural ramp |
| Cordon de l'épaulement | **C1** | **3** : entre CIF et C2 | Epaulement | Shoulder cord | **P1** | **3** : between IP and P2 | Shoulder |
| Cordon 2 | **C2** | **4** : entre C1 et C3 | Partie convexe du tour | Cord 2 | **P2** | **4** : between P1 and P3 | Convex part of the whorl |
| Cordon 3 | **C3** | **5** : entre C2 et C4 | Partie convexe du tour | Cord 3 | **P3** | **5** : between P2 and P4 | Convex part of the whorl |
| Cordon 4 | **C4** | **6** : entre C3 et C5 | Partie convexe du tour ou canal siphonal | Cord 4 | **P4** | **6** : between P3 and P5 | Convex part of the whorl or siphonal canal |
| Cordon 5 | **C5** | **7** : entre C4 et C6 | Partie convexe du tour ou canal siphonal | Cord 5 | **P5** | **7** : between P4 and P6 | Convex part of the whorl or siphonal canal |
| Cordon 6 | **C6** | **8** : entre C5 et CSP | Partie convexe du tour ou canal siphonal | Cord 6 | **P6** | **8** : between P5 and ADP | Convex part of the whorl or siphonal canal |
| Cordon siphonal adapical | **CSP** | **9** : entre C6 et CSM | Canal siphonal | Adapical siphonal cord | **ADP** | **9** : between P6 and MP | Siphonal canal |
| Cordon siphonal médian | **CSM** | **10** : entre CSP et CSA | Canal siphonal | Median siphonal cord | **MP** | **10** : between ADP and ABP | Siphonal canal |
| Cordon siphonal abapical (standard) | **CSA** | **11** : Entre CSM et CSA1 | Canal siphonal | Abapical siphonal cord (standard) | **ABP** | **11** : between MP and EAB | Siphonal canal |
| Cordon siphonal abapical 1 | **CSA1** | **12** : entre CSA et CSA2 | Canal siphonal (présent chez *Murex* et *Siratus*) | Extreme abapical siphonal cord 1 | **EAB1** | **12** : between ABP and EAB2 | Siphonal canal (present in *Murex* and *Siratus*) |
| Cordon siphonal abapical 2 | **CSA2** | **13** : entre CSA1 et CSA3 | Canal siphonal (présent chez *Murex*) | Extreme abapical siphonal cord 2 | **EAB2** | **13** : between EAB and EAB3 | Siphonal canal (present in *Murex*) |
| Cordon siphonal abapical 3 | **CSA3** | 14 : abapical à CSA2 | Canal siphonal (présent chez *Murex*) | Extreme abapical siphonal cord 3 | **EAB3** | **14** : abapical to EAB2 | Siphonal canal (present in *Murex*) |

**Table 1** : French and english terminology used to describe the primary cords regarding their ontogenetical and topological correspondences.

| **FRENCH (Merle, 1999)** | | | **ENGLISH** | | |
|---|---|---|---|---|---|
| **CORDONS SECONDAIRES (Fig. 4)** | | | **SECONDARY CORDS (Fig. 4)** | | |
| **Cordons** | **Abre-viation** | **Position topologique** | **Cords** | **Abbre-viation** | **Topological place** |
| Cordon infrasutural adapical | **cifp** | Adapical à CIF | Adapical infrasutural cord | **adis** | Adapical to IP |
| Cordon infrasutural abapical | **cifa** | Entre CIF et C1 | Abapical infrasutural cord | **abis** | Between IP and P1 |
| Cordon 1 | **ci1** | Entre C1 et C2 | Cord 1 | **s1** | Between P1 and P2 |
| Cordon 2 | **ci2** | Entre C2 et C3 | Cord 2 | **s2** | Between P2 and P3 |
| Cordon 3 | **ci3** | Entre C3 et C4 | Cord 3 | **s3** | Between P3 and P4 |
| Cordon 4 | **ci4** | Entre C4 et C5 | Cord 4 | **s4** | Between P4 and P5 |
| Cordon 5 | **ci5** | Entre C5 et C6 | Cord 5 | **s5** | Between P5 and P6 |
| Cordon 6 | **ci6** | Entre C6 et CSP | Cord 6 | **s6** | Between P6 and ADP |
| Cordon siphonal adapical | **cisp** | Entre CSP et CSM | Adapical siphonal cord | **ads** | Between ADP and MP |
| Cordon siphonal médian | **cism** | Entre CSM et CSA | Median siphonal cord | **ms** | Between MP and ABP |
| Cordon siphonal abapical (standard) | **cisa** | Entre CSA entre CSA1 | Abapical siphonal cord (standard) | **abs** | Between ABP and EAB |
| Cordon siphonal abapical 1 | **cisa 1** | Entre CSA1 et CSA2 | Extreme abapical siphonal cord 1 | **eabs1** | Between EAB and EAB2 |
| Cordon siphonal abapical 2 | **cisa 2** | Entre CSA2 et CSA3 | Extreme abapical siphonal cord 2 | **eabs 2** | Between EAB2 and EAB3 |

**Table 2** : French and english terminology used to describe the secondary cords regarding their ontogenetical and topological correspondences.

## INTERNAL DENTICLES OF THE OUTER LIP

The internal denticles of the outer lip (Table 3) seem to be negative prints of the main spiral sculptures (primary cords) on the dorsal face (Fig. 5), and each denticle generally corresponds to a groove splitting two primary cords (Fig. 6). However, the construction of the denticles also depends to the ability that the muricids have to secrete the microstructural layers of shelly material, necessary to amplify the internal relief of the groove. Consequently, the too thin shells, such as the juvenile muricids, or the too thin parts of the shell, such as the siphonal canal, lack internal denticles. Despite a relationship between the major spiral grooves and the secretion of shelly material in these grooves, the distribution of the internal denticles does not always respect the correlation majors grooves/denticle. Two main deformations may occur and generate a potential pittfall to identify each denticles if the topological places of the denticles are only considered.

The first deformation is the splitted denticles (Fig. 7). This kind of deformation has been reported, and already Deshayes (1835 : 593-594), describing *Murex rudis* (=*M. subrudis* d'Orbigny, 1850), noted the presence of splitted denticles in the outer lip of this species. The splitted denticles frequently occur when the internal shelly material is too thin to build a complete denticle and particularly, when a secondary cord generates two secondary grooves, between two primary cords. The second deformation is the opposite and generates the loss or the fusion of a denticle (Fig. 8). This case occurs when two primary cords are so contracted, that the groove splitting these two cords become reduced. Consequently to the reduction of this groove, the internal relief becomes too straight to individualize a denticle during the deposit of the shelly material.

| FRENCH (Merle, 1999) | | | ENGLISH | | |
|---|---|---|---|---|---|
| DENTS INTERNES DU LABRE (Fig. 6) | | | INTERNAL DENTICLES OF THE OUTER LIP (Fig. 6) | | |
| **Dents** | **Abreviation** | **Position topologique** | **Denticles** | **Abbreviation** | **Topological place** |
| Dent infrasuturale | **DI** | 1 : rampe infrasuturale sur la face ventrale | Infrasutural denticle | **ID** | 1 : infrasutural ramp on the ventral face |
| Dent 1 de la partie convexe du tour | **D1** | 2 : entre C1 et C2 sur la face ventrale | Denticle 1 of the convex part of the whorl | **D1** | 2 : between P1 and P2 on the ventral face |
| Dent 2 de la partie convexe du tour | **D2** | 3 : entre C2 et C3 sur la face ventrale | Denticle 2 of the convex part of the whorl | **D2** | 3 : between P2 and P3 on the ventral face |
| Dent 3 de la partie convexe du tour | **D3** | 4 : entre C3 et C4 sur la face ventrale | Denticle 3 of the convex part of the whorl | **D3** | 4 : between P3 and P4 on the ventral face |
| Dent 4 de la partie convexe du tour | **D4** | 5 : entre C4 et C5 sur la face ventrale | Denticle 4 of the convex part of the whorl | **D4** | 5 : between P4 and P5 on the ventral face |
| Dent 5 de la partie convexe du tour | **D5** | 6 : entre C5 et C6 sur la face ventrale | Denticle 5 of the convex part of the whorl | **D5** | 6 : between P5 and P6 on the ventral face |
| Dent 6 de la partie convexe du tour | **D6** | 7 : entre C6 et CSP sur la face ventrale | Denticle 6 of the convex part of the whorl | **D6** | 7 : between P6 and ADP on the ventral face |

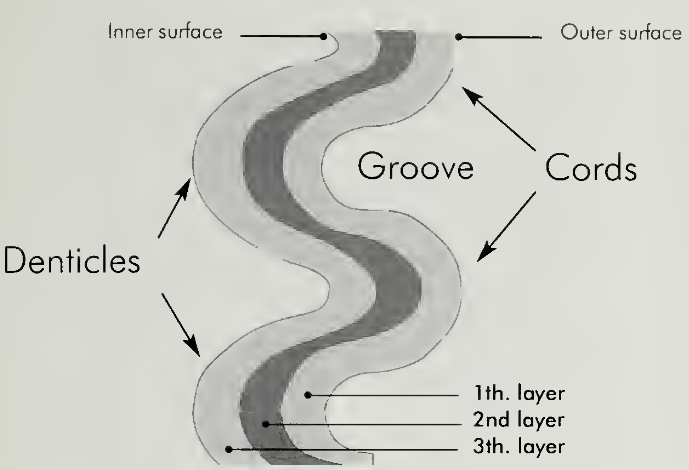
**Table 3** : French and english terminology used to describe the internal denticles of the outer lip regarding their ontogenetical and topological correspondences.

**Figure 5** : Drawing of the sagittal section of an outer lip. Its shows the topographical relation between the internal denticles inside the aperture and the external relief of the spiral sculpture (grooves and cords).

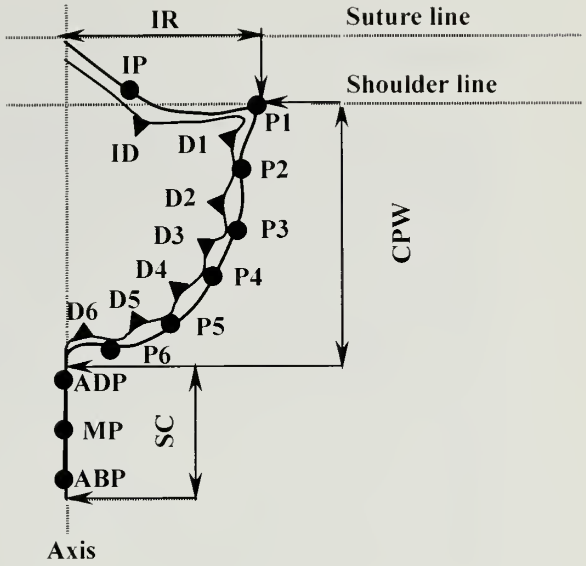
**Figure 6** : Arrangement and maximum number of the major internal denticles of the outer lip (apertural view). IR = sutural ramp ; CPW= convex part of the whorl ; SC = siphonal canal. The circles indicate the place of the primary cords and the triangles indicate the place and the internal denticles.

**Figure 7** : Drawing of three sagittal sections of the outer lip. It shows the construction of a splitted internal denticle (D*a*). Step 1 : non splitted denticle (D*a*) corresponding to the groove between the primary cords P*a* and P*b* ; step 2 : D*a* partially splitted and appearance of a secondary cord s*a* between P*a* and P*b* ; step 3 : D*a* splitted and increase of the relief of the secondary cord s*a*.

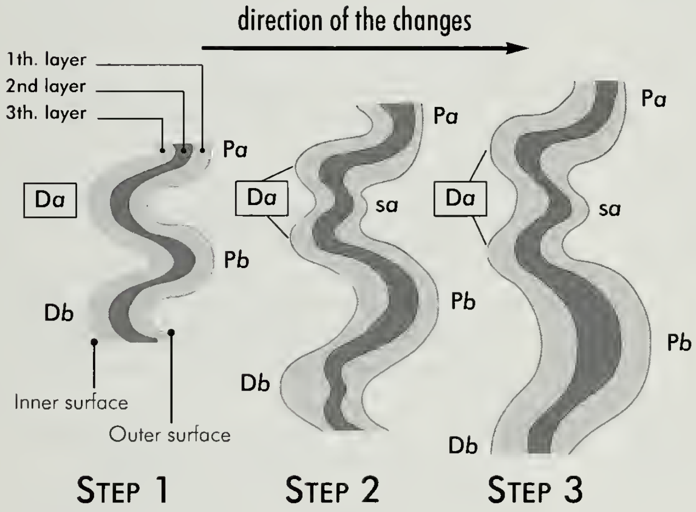
**Figure 8** : Drawing of three sagittal sections of the outer lip. It shows the possibility of fused denticles (D*a* and D*b*). Step 1 : D*a* and D*b* are well individualized ; step 2 : D*a* and D*b* are contracted and also P*a* and P*b*, the groove between P*a* and P*b* is narrow ; step 3 : D*a* is not very distinct from D*b*. The morphology of the internal denticles D*a* and D*b* in the steps 2 and 3 gives the wrong impression of a single splitted denticle.


Inner surface
Outer surface
Groove
Cords
Denticles
1th. layer
2nd layer
3th. layer

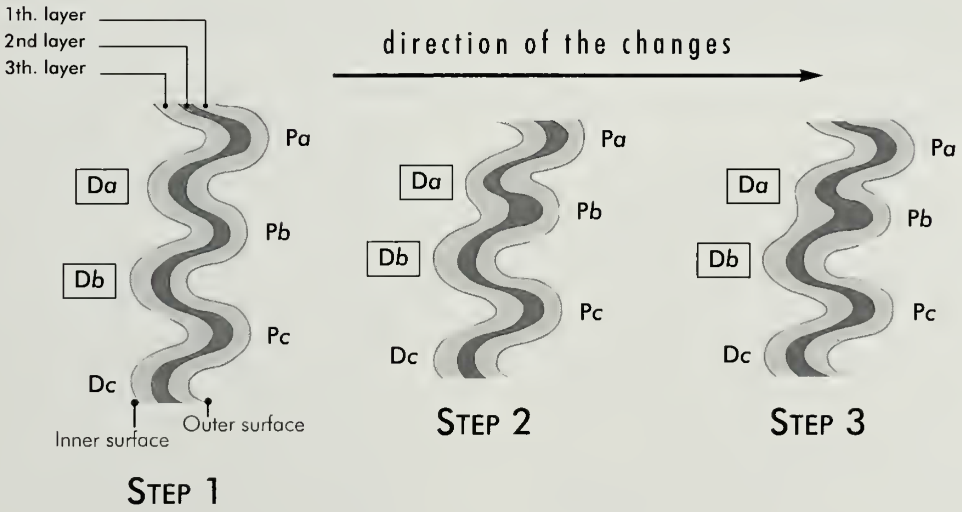
5


IR
Suture line
IP
Shoulder line
ID
D1
P1
P2
D2
D3
P3
CPW
D4
P4
D5
D6
P5
P6
ADP
MP
SC
ABP
Axis

6


direction of the changes
1th. layer
2nd layer
3th. layer
Pa
Da
Pb
Db
Inner surface
Outer surface
Pa
Da
sa
Pb
Db
Pa
Da
sa
Pb
Db
STEP 1
STEP 2
STEP 3

7


1th. layer
2nd layer
3th. layer
direction of the changes
Pa
Da
Pb
Db
Pc
Dc
Inner surface
Outer surface
STEP 1
Pa
Da
Pb
Db
Pc
Dc
STEP 2
Pa
Da
Pb
Db
Pc
Dc
STEP 3

8

## CONCLUSION

The muricid shells have been regarded as a potential taxonomic pitfall, because of too much homoplastic characters (Harasewych, 1984 ; Kool, 1993a, 1993b ; Bouchet & Houart, 1994, 1996 ; Vermeij & Kool, 1994). However, the concept of homology has been unsufficiently applied in the muricid shell descriptions (Hylleberg & Nateewathana, 1992 ; Miller, 1999 and Merle, 1999). Therefore, a superficial definition of the shell characters generates the risk of taxonomic mistakes and amplifies the idea that they are too much homoplastic to be used (Miller, 1999, Merle, 1999). These observations strongly suggest that the traditional descriptive method is inacurate to correctly analyse the phylogenetic, the taxonomic and the evolutionary aspects of the muricid shells. The morphological approach consisting to identify the spiral characters by their ontogenetical and topological correspondences is given in this paper and demonstrates that the descriptive method may be performed. With the analyse of the constructional characters (Miller, 1999), this approach attempts to bring a better definition and a clearer presentation of the shell characters and to increase the importance of the concept of homology in the descriptive method.

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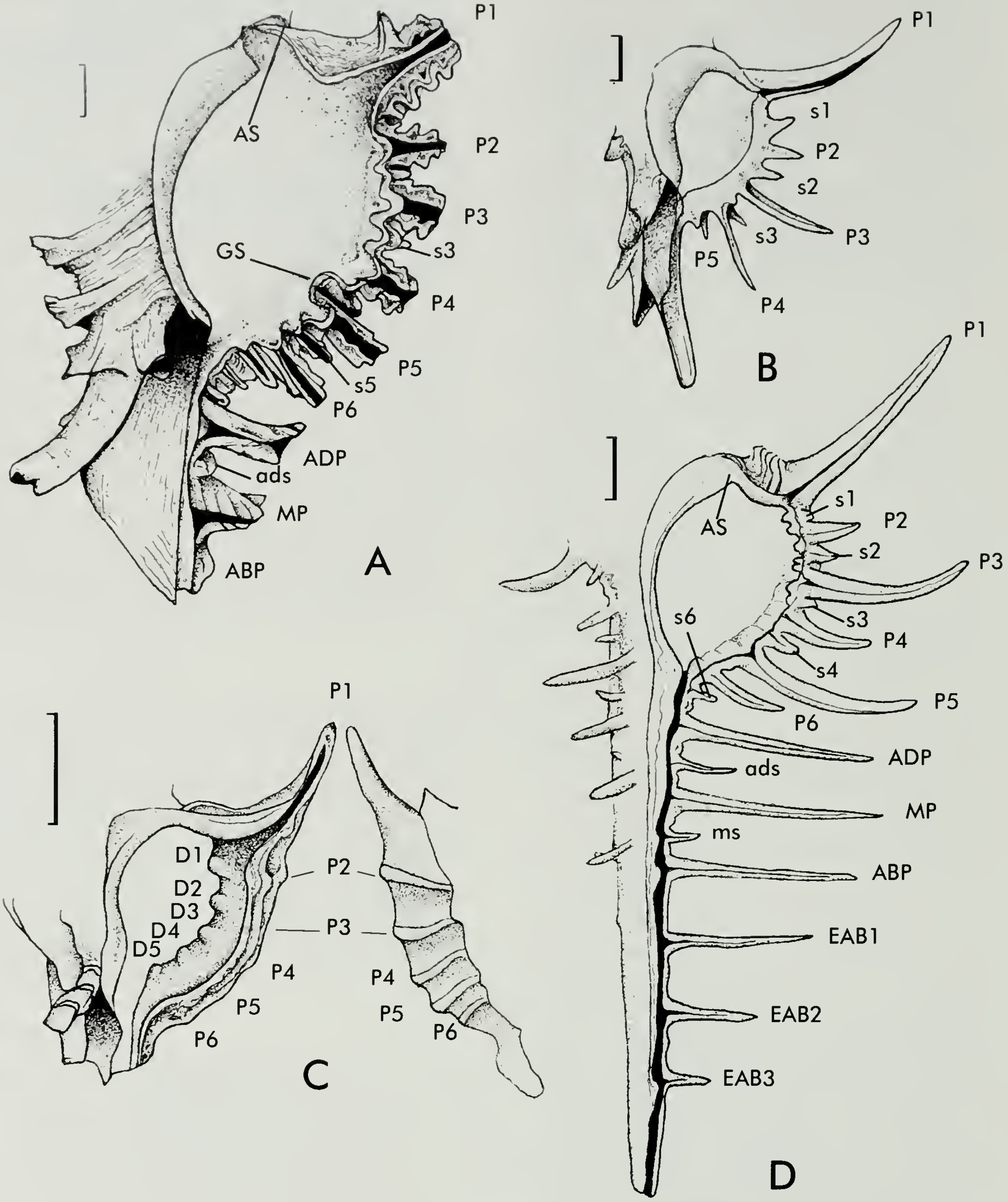

**Figure 9** : Spiral sculpture (apertural view) of Muricinae (*Chicoreus*, *Poirieria*, *Flexopteron* and *Murex*). A : *Chicoreus ramosus* (Linnaeus, 1758), Thailand, DME ; B : *Poirieria zelandica* (Quoy & Gaimard, 1833), Cook Strait (New Zealand), holotype, MNHN-BIMM ; C : *Flexopteron primanova* (Houart, 1985), Madagascar, holotype, MNHN-BIMM ; D : *Murex tribulus* (Linnaeus, 1758), East Asia, NHM, lectotype. AS = anal sulcus ; GS = groove spine ; scale bar : 5 mm.

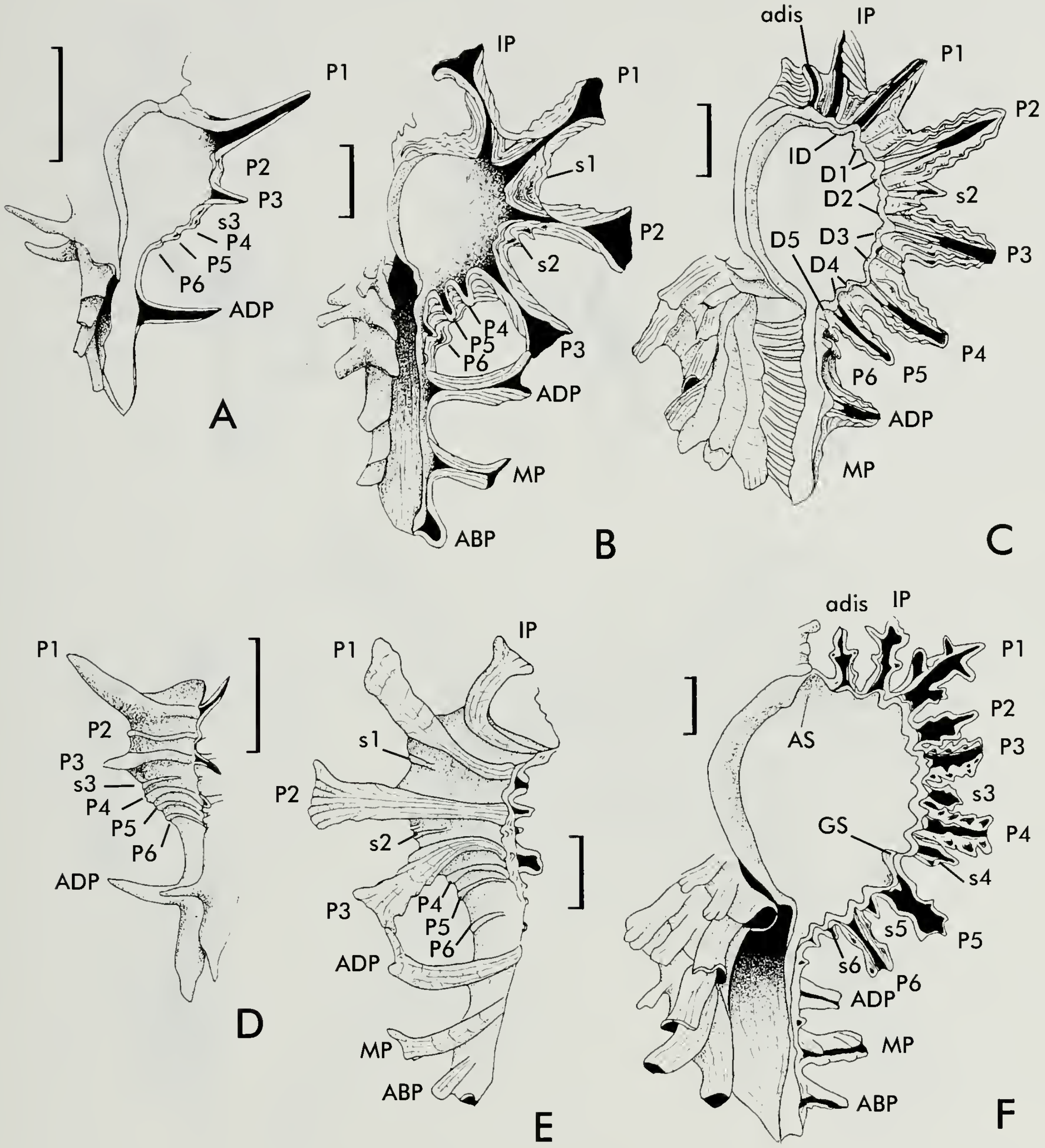

**Figure 10** : Spiral sculpture of Muricinae (*Paziella*, *Homalocantha* and *Hexaplex*). A, D (D = dorsal view) : *Paziella pazi*, Tampa (Floride), MNHN-BIMM ; B, E (E = dorsal view) : *Homalocantha scorpio* (Linnaeus, 1758), Australie, MNHN-BIMM ; C : *Homalocantha melanomathos* (Gmelin, 1791), Cuba, MNHN-BIMM ; F : *Hexaplex cichoreum* (Gmelin, 1791), Philippines, DME. GS = groove spine ; scale bar : 5 mm.

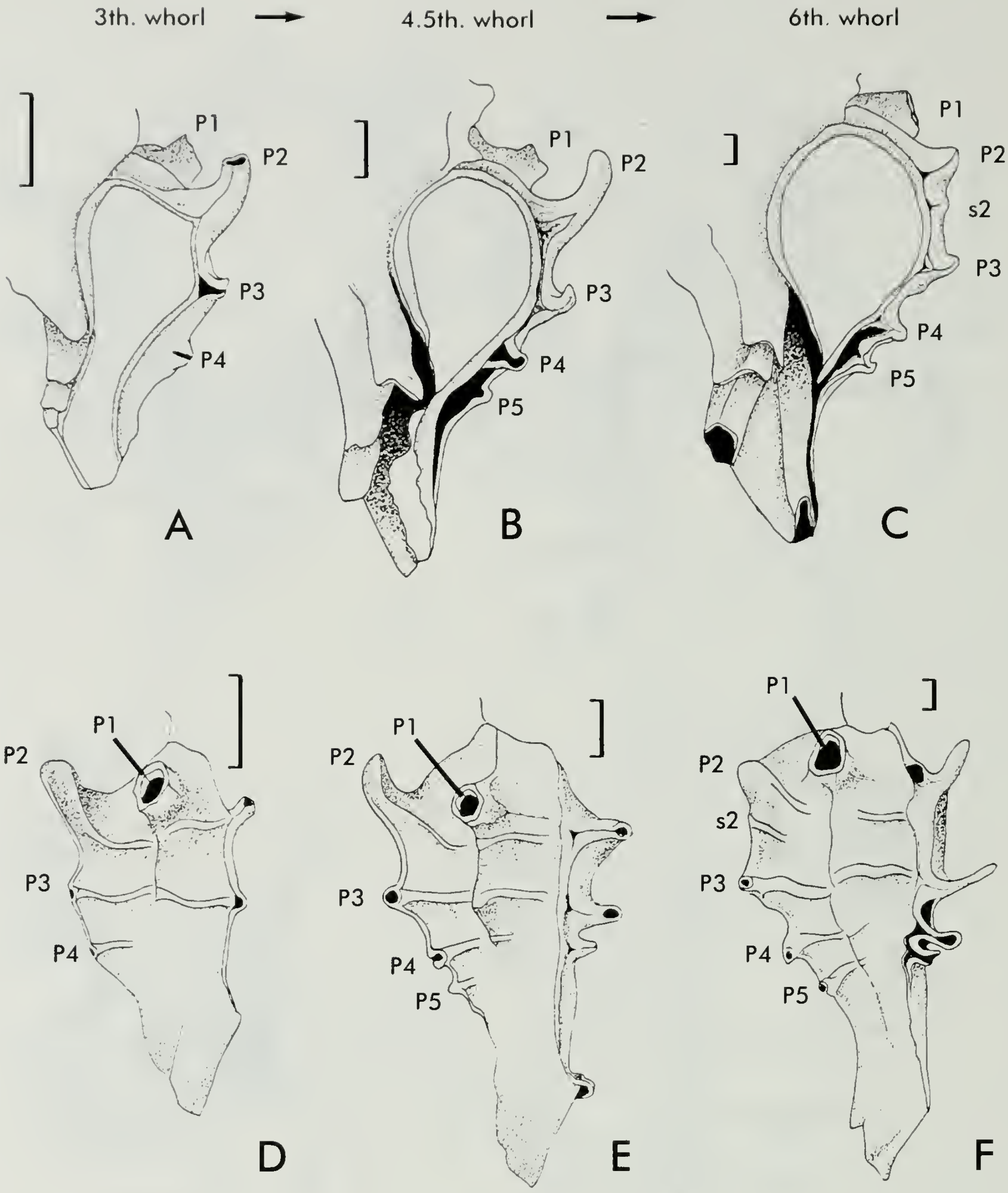

**Figure 11** : Ontogenesis and spiral sculpture of *Typhis tubifer* (Bruguière, 1792), Lutetian, Paris Basin. A, D (D = dorsal view) : Parnes, MNHN-LP (coll. Roissy); B-C, E-F (E-F = dorsal views), Villiers-St-Frédéric, DME. Scale bar : 1 mm.

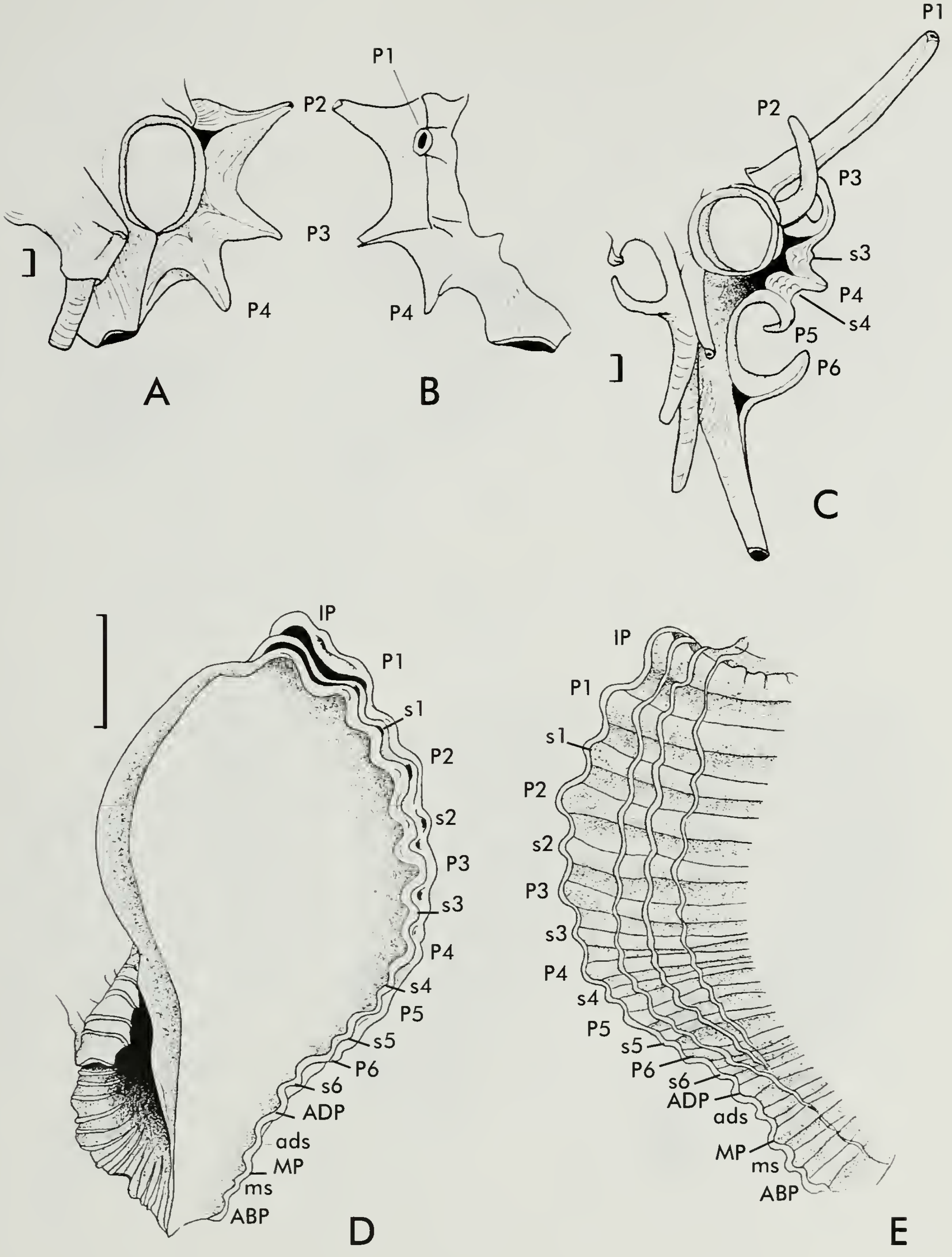

**Figure 12** : Spiral sculpture of Typhinae (*Typhis* and *Monstrotyphis*) and Trophoninae (*Trophon*). A-B (B = dorsal view): *Typhis horridus* (Brocchi, 1814), Pliocene, Italia, DME ; C : *Monstrotyphis tosaensis* (Azuma, 1960), Shikoku Island, Japan ; D-E (E = dorsal view): *Trophon geversianus* (Pallas, 1774), Magellan Strait, MNHN-BIMM. Scale bars : 1 mm for the Typhinae and 5 mm for *T. geversianus*.

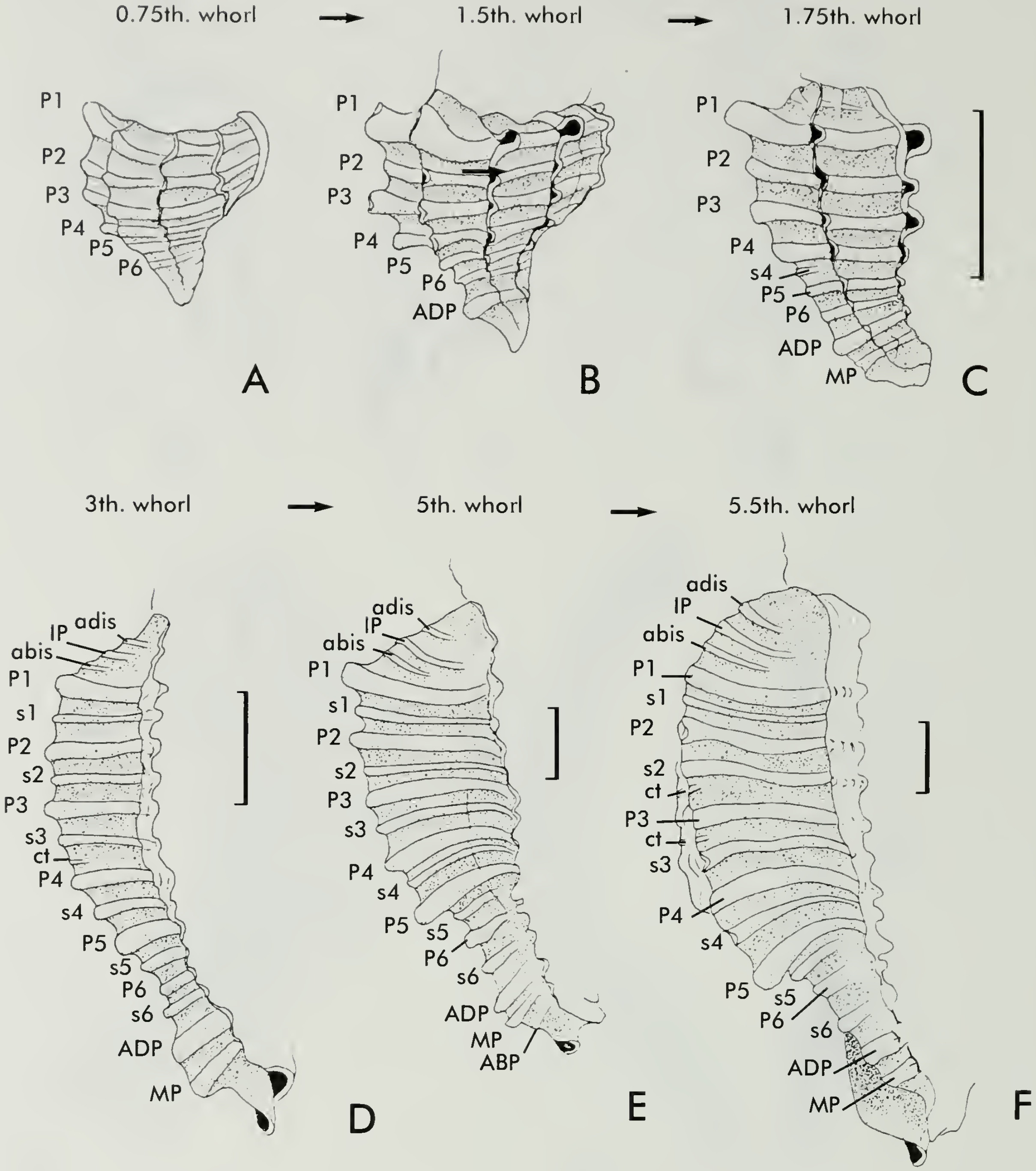

**Figure 13** : Ontogenesis and spiral sculpture (dorsal view) of the Muricopsinae, *Murexsul elatospira* (Cossmann & Peyrot 1923), Chattian, Aquitaine Basin. A-D, F : Peyrehorade (Peyrère), MNHN-BIMM (coll. Lozouet & Maestrati), E : Peyrehorade (Peyrère), MNHN-LP, holotype, coll. Cossmann. Scale bar : 1 mm.

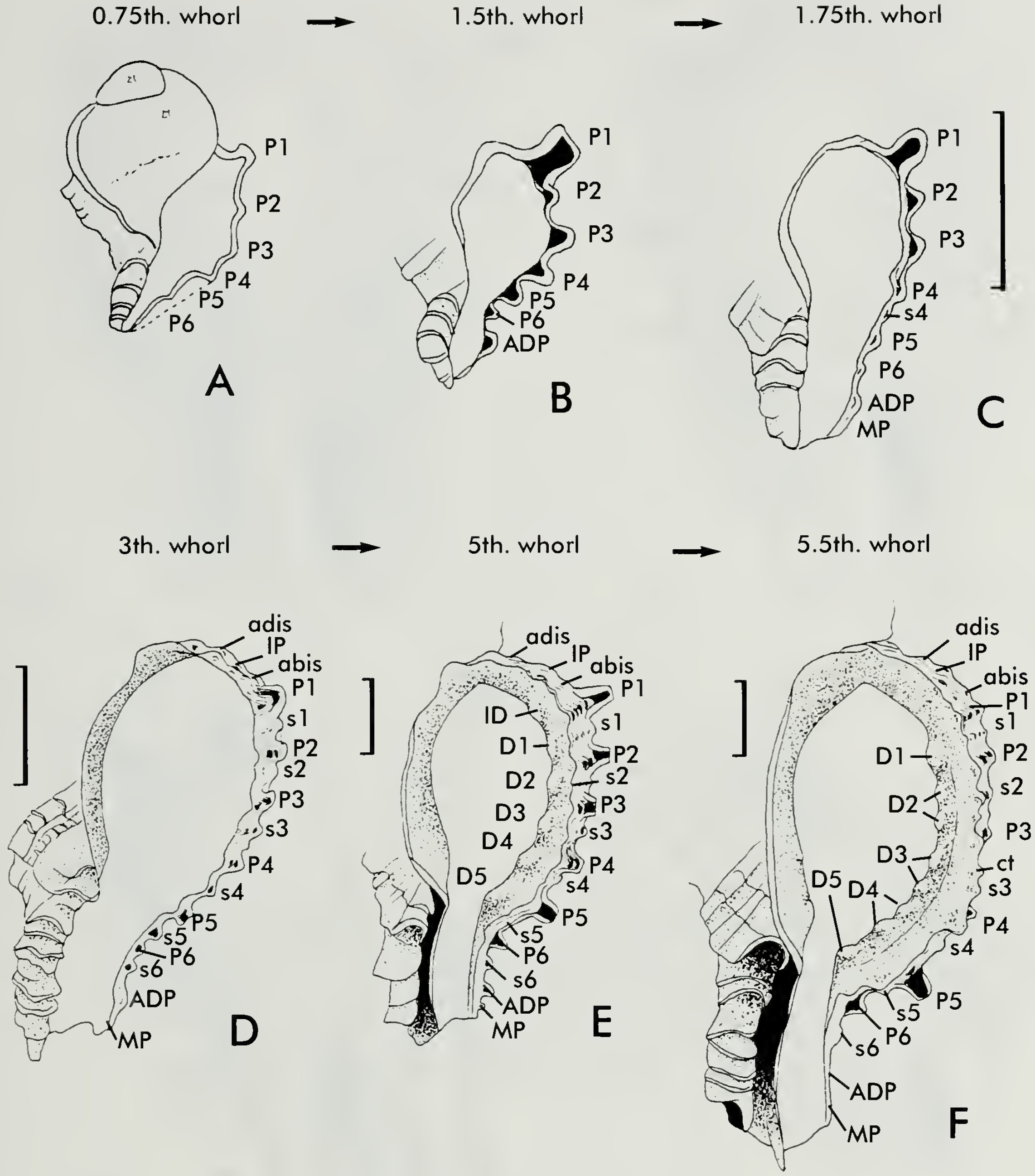

**Figure 14** : Ontogenesis and spiral sculpture (ventral view) of the Muricopsinae, *Murexsul elatospira* (Cossmann & Peyrot 1923), Chattian, Aquitaine Basin. A-D, F : Peyrehorade (Peyrère), MNHN-BIMM (coll. Lozouet & Maestrati), E : Peyrehorade (Peyrère), MNHN-LP, holotype, coll. Cossmann. Scale bar : 1 mm.

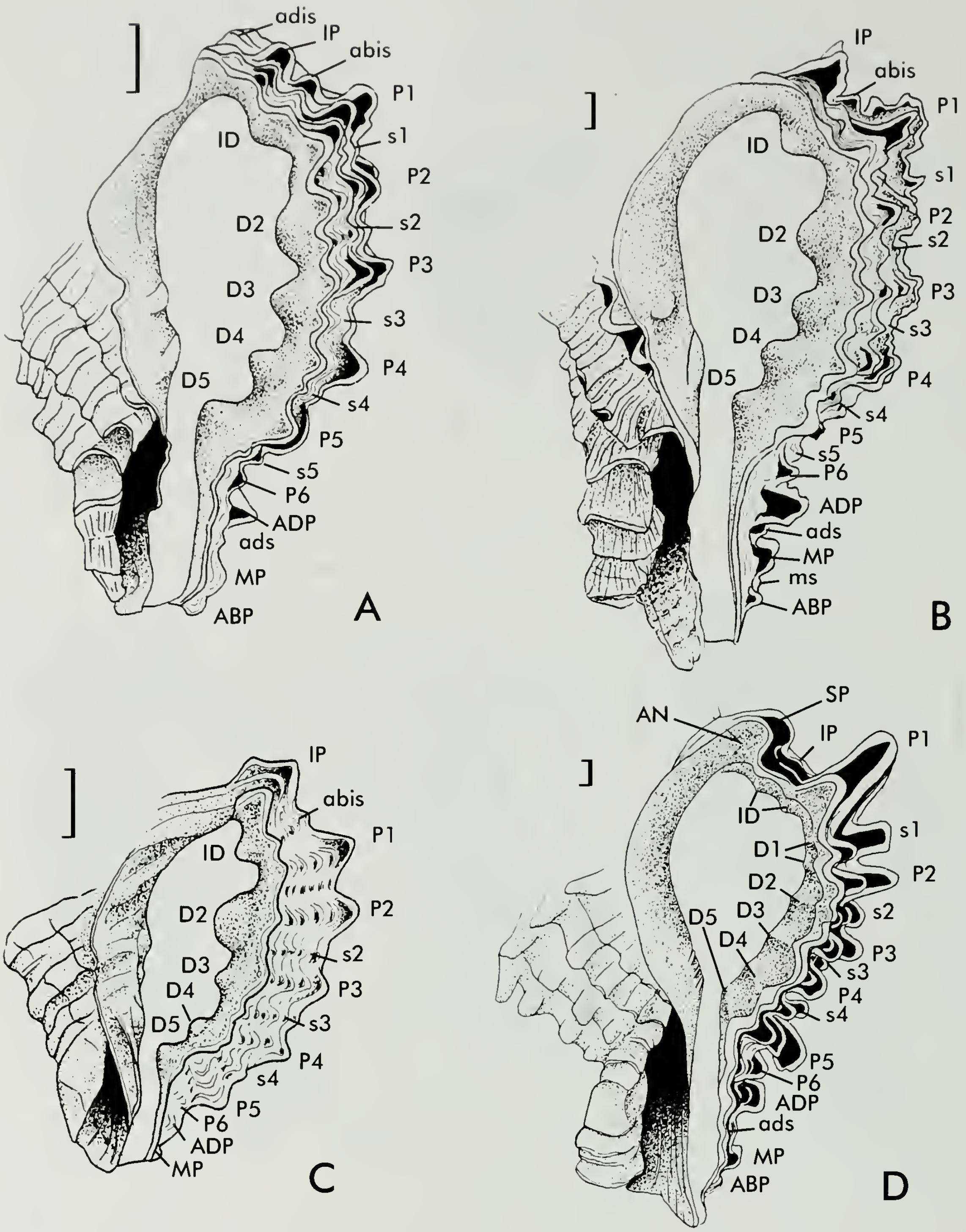

**Figure 15** : Spiral sculpture (ventral view) of Muricopsinae (*Muricopsis* and *Acanthotrophon*). A : *Muricopsis (s.s.) cristata* (Brocchi, 1814), Collioure, France, DME ; B : *M. (s.s.) cristata*, Pliocene, Sienna (Italy) ; C : *M. (Risomurex) deformis* (Reeve, 1846), Punta Cahuita (Costa Rica), USNM (d'après Vokes & Houart, 1986) ; D : *Acanthotrophon carduus* (Broderip, 1833), Cantadora Island, LDO. AN = anal notch ; scale bar : 1 mm.

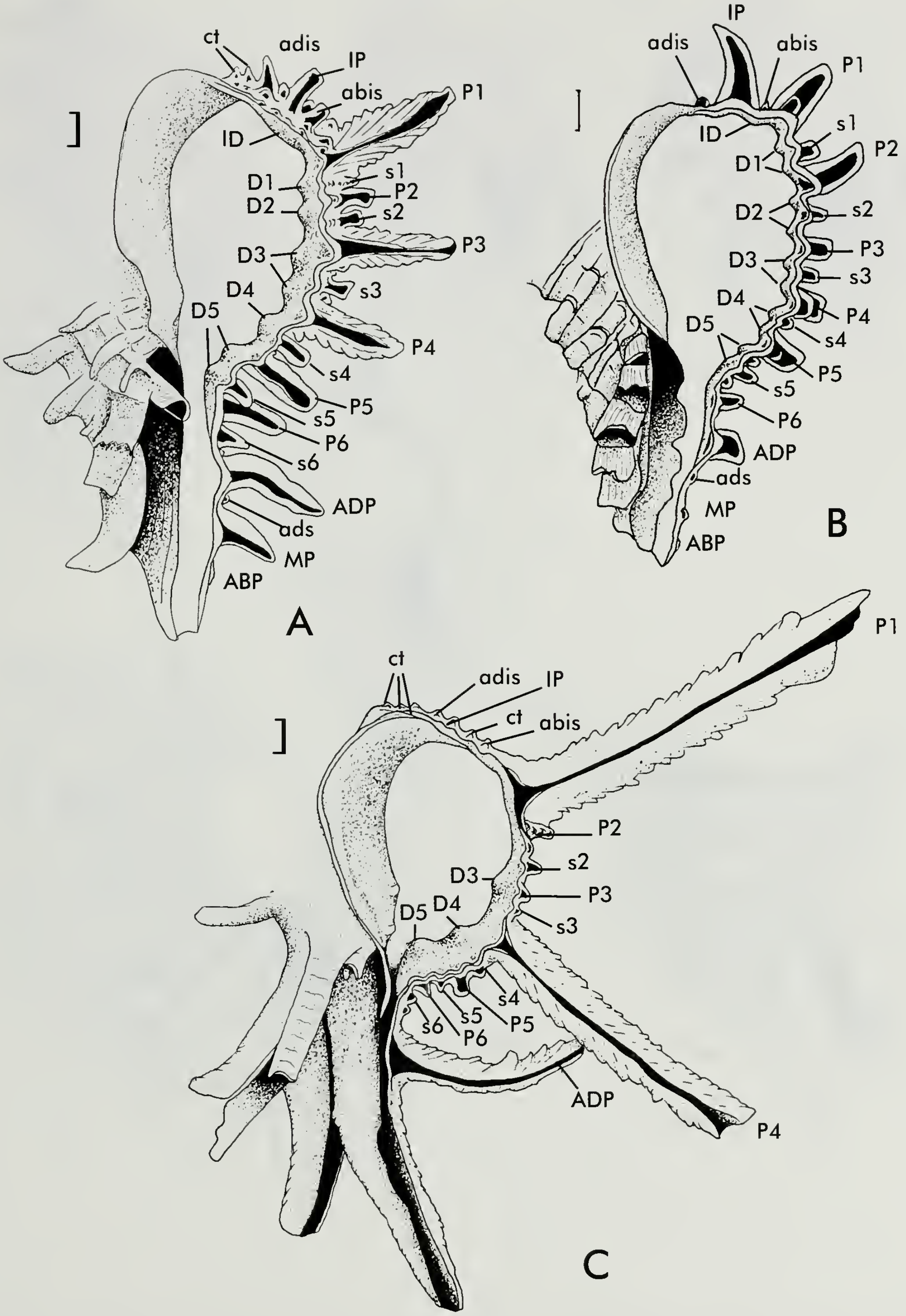

**Figure 16** : Spiral sculpture (ventral view) of Muricopsinae (*Murexsul* and *Xastilia*). A : ?*Murexsul oxytatus* (Smith, 1938) : St-Thomas, Virgin Island (USA), MNHN-BIMM ; B : *Murexsul octogonus* (Quoy & Gaimard, 1833), Pleistocene, Castlecliff (New-Zealand), MNHN-LP ; C : *Xastilia kosugei* Bouchet & Houart, 1994 : Coral Sea (S. W. Pacific), MNHN-BIMM, holotype. Scale bar : 1 mm.

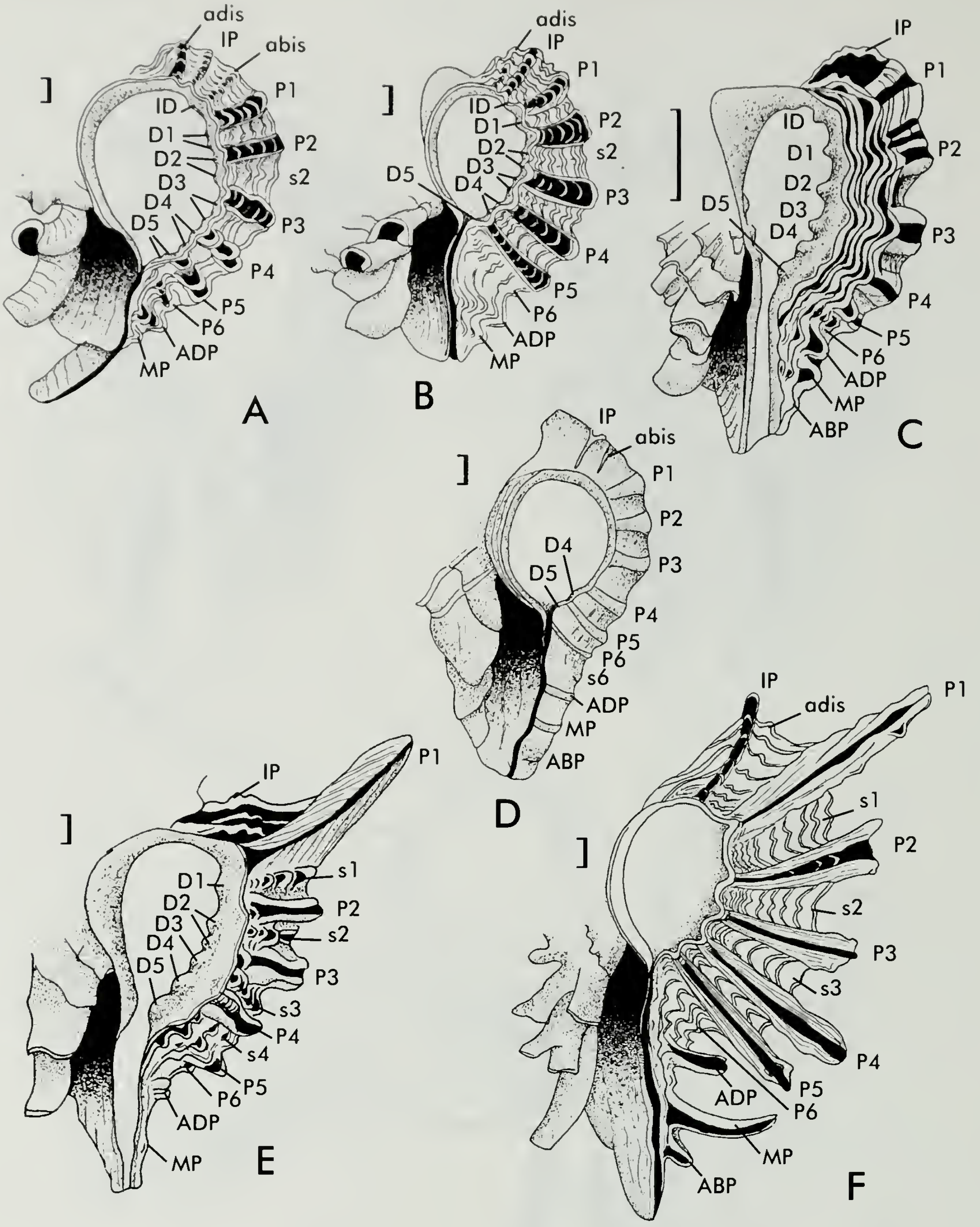

**Figure 17** : Spiral sculpture (ventral view) of Muricopsinae (*Favartia (s.s.)*, *F. (Caribiella)*, *Pygmaepterys*, *Maxwellia*, *Pazinotus* and *F. (Murexiella)*. A : *Favartia (s.s.) brevicula* (Sowerby, 1834), Mauritius Island, MNHN-BIMM ; B : *F. (Caribiella) alveata* (Kiener, 1842), Mexico, MNHN-BIMM ; C : *Pygmaepterys germainae* Vokes & d'Attilio, 1980, Colon, USNM (paratype) ; D : *Maxwellia gemma* (Sowerby, 1879), Newport, California, MNHN-BIMM ; E : *Pazinotus sibogae* (Schepman, 1911), Coral Sea (Nova Banks), MNHN-BIMM ; F : *F. (Murexiella) hidalgoi* (Crosse, 1869), Tampa, Florida, MNHN-BIMM. Scale bar : 1 mm.

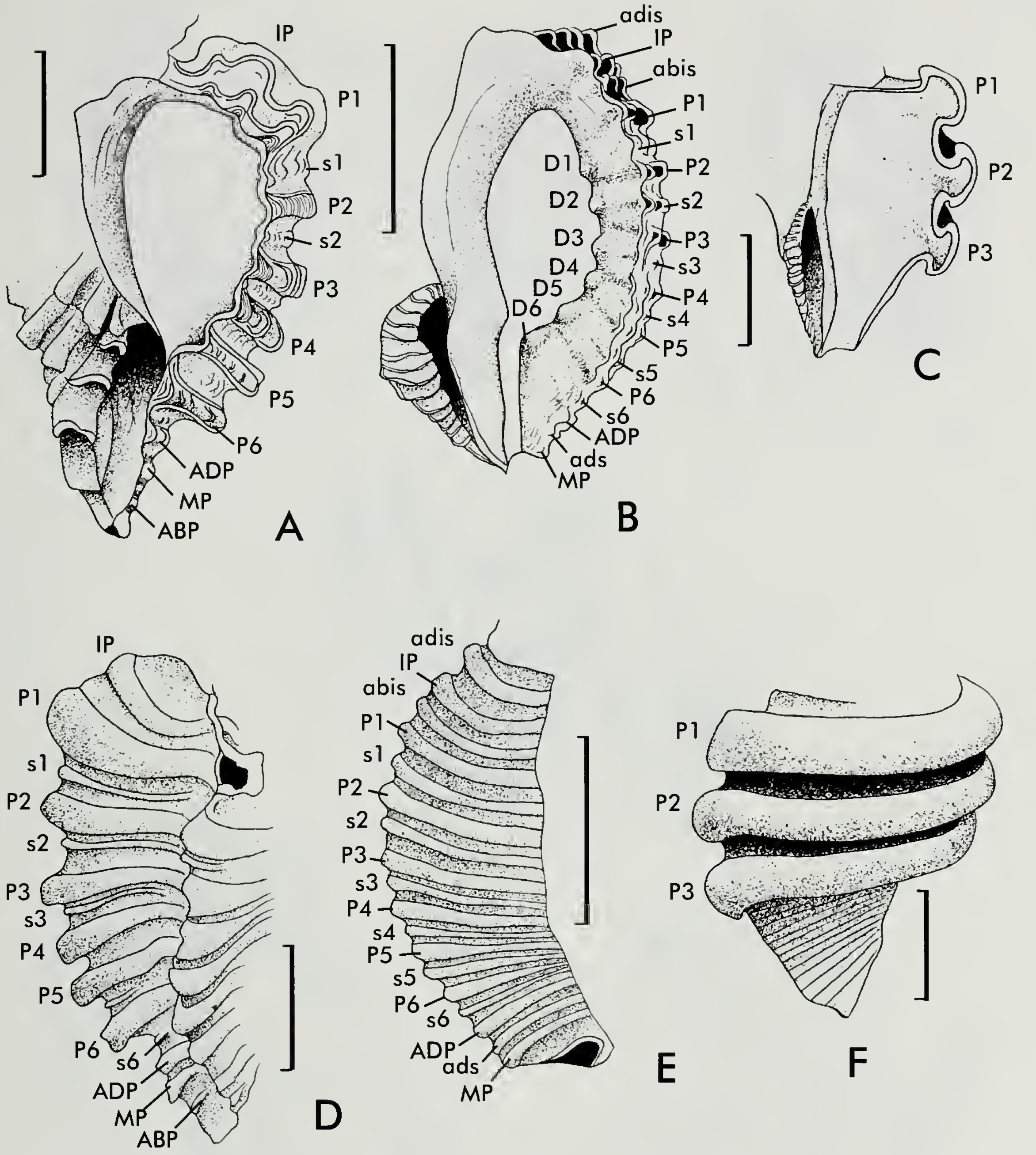

**Figure 18** : Spiral sculpture of Ocenebrinae (*Ocenebra*, *Nucella* and *Trochia*). A, E (E = dorsal view) : *Ocenebra erinaceus* (Linnaeus, 1758), Aigues Mortes, France, DME ; B, F (F = dorsal view) : *Nucella lapillus* (Linnaeus, 1758), Quiberon, France, DME ; C-D (D = dorsal view) : *Trochia cingulata* Linnaeus, 1771, False Bay, South Africa, MNHN-BIMM. Scale bar : 5 mm.

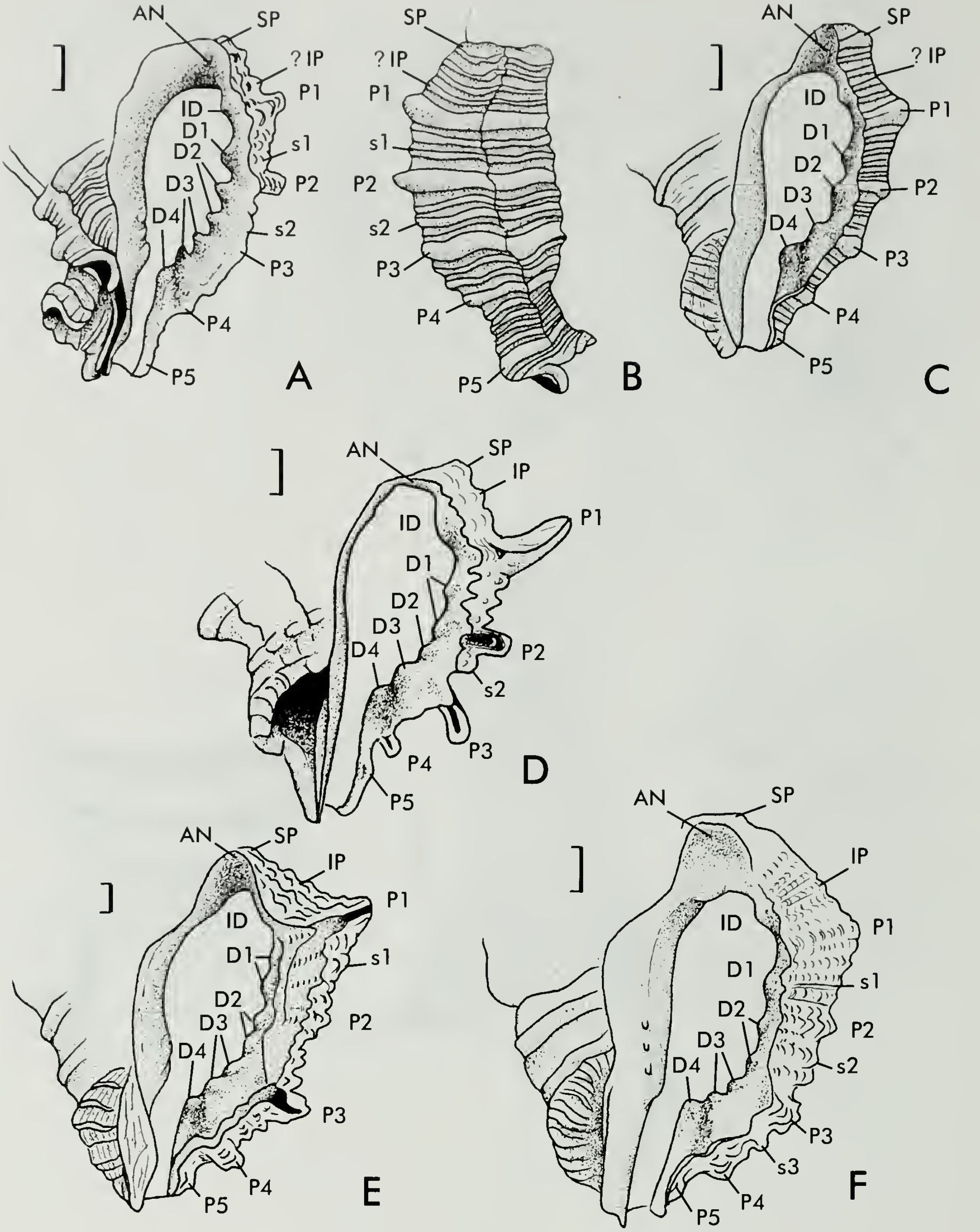

**Figure 19** : Spiral sculpture of Ergalataxinae (*Orania*, *Spinidrupa*, *Muricodrupa* and *Ergalatax*). A-B (B = dorsal view) : *Orania archea* Houart, 1995, Samar, Philippines, MNHN-BIMM, C : *O. dharmai* Houart, 1995, Borneo, MNHN-BIMM ; *Spinidrupa euracantha* (Adams, 1853), Tahiti, RH ; *Muricodrupa fenestrata* (Blainville, 1832), New-Caledonia, RH ; *Ergalatax obscura* Houart, 1996, Djibouti, MNHN-BIMM. AN = anal notch ; scale bar : 1 mm.

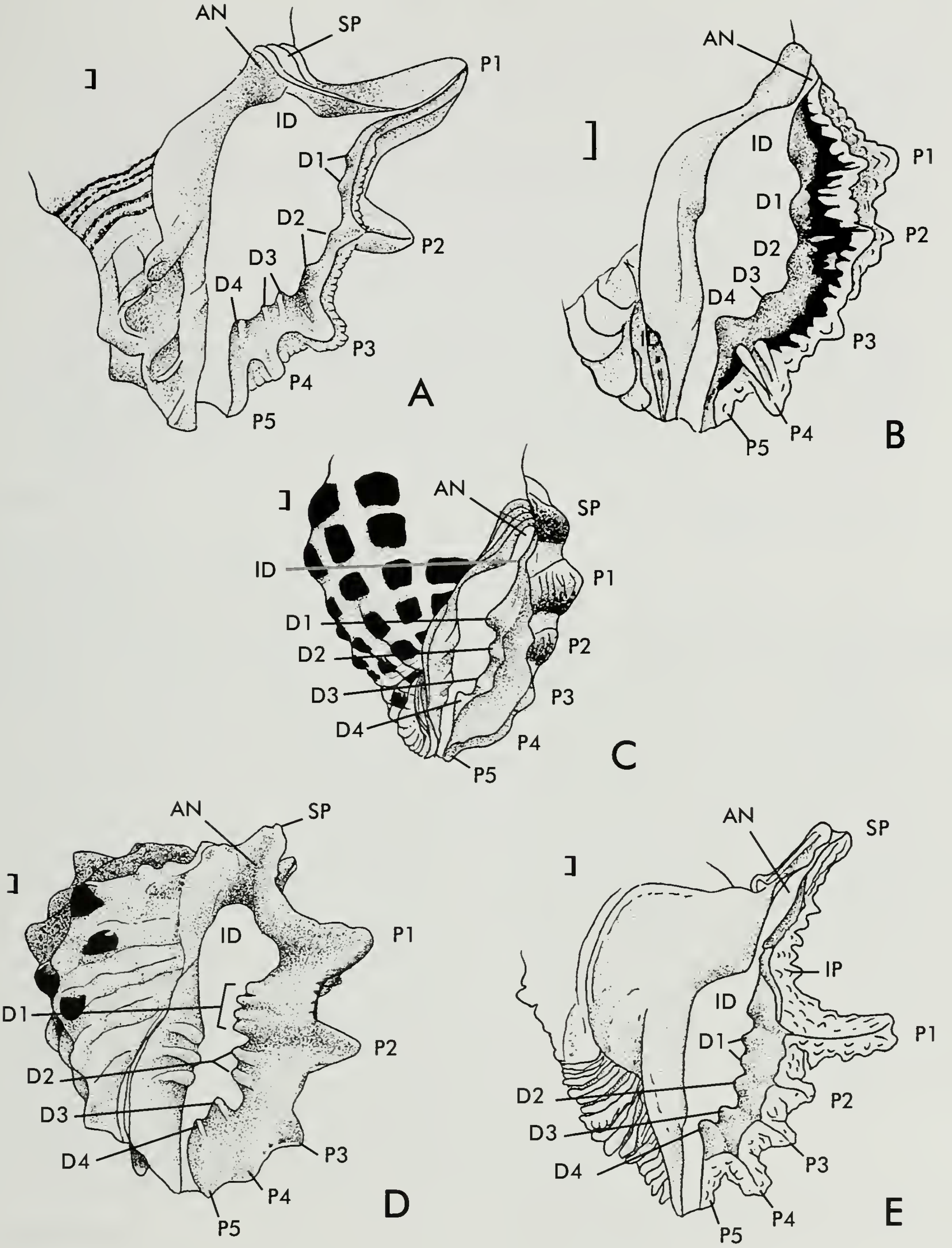

**Figure 20** : Spiral sculpture (ventral view) of Rapaninae (*Stramonita*, *Thaisella*, *Morula*, *Drupa* and *Drupina*). A : *Stramonita armigera* (Link, 1807), Tahiti, JT ; B : *Thaisella foliacea* (Conrad, 1837), Tahiti, JT ; C : *Morula granulata* (Duclos, 1832), Fiji ; D : *Drupa morum* (Röding, 1798), Mariana Island ; E : *Drupina glossularia* (Röding, 1798), Fiji. A-B after Tröndle & Houart (1992), C and E after Cernohorsky (1969). AN = anal notch ; scale bar : 1 mm.